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# Description of four new species of *Ledella* Verrill and Bush, 1897 (Pelecypoda: Nuculanidae) off the coast of Brazil, using a morphometric approach

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**Abstract:** As a result of deep-water oil prospecting in the Campos Basin, Brazil, a rich diversity of protobranchiate pelecypods has been revealed. In this study, we identified four new species of *Ledella* and conducted a morphometric study to corroborate their delimitation. The resulting conchological-based statistic models are in 95% agreement with the traditional criteria for the right valves and 88.33% for the left valves. Certain variables were particularly relevant in these analyses; these variables expressed the importance of the shape of the rostrum and hinge plate for the right valves and the general shell shape and hinge plate for the left valves. The hinge plate variables are not typically used as diagnostic characters of protobranchiate pelecypods and, when applied, they are not given much importance. However, our statistical analyses stressed the importance of these characters. Therefore, we strongly suggest that future descriptions of protobranchiate pelecypods place greater emphasis on these characters.

**Key words:** Biodiversity, deep sea, hinge plate, morphometry, Bivalvia.

As a consequence of oil prospecting in the Campos Basin (20–23°S) by the oil company Petrobras, deep-water samples have been obtained, which have increased our knowledge of deep-sea mollusks from the southeast of Brazil over the last 10 years (*e.g.*, Domaneschi and Lopes 1990, Absalão *et al.* 2003, Caetano *et al.* 2006, Zelaya *et al.* 2006, Simone and Cunha 2008, Oliveira and Absalão 2009, Passos and Birman 2009, Figueira and Absalão 2010).

Protobranchia is the most abundant group of Pelecypoda in the deep-sea (400–5000 m), which constitutes the largest habitat on Earth, with at least 94% of the seabed lying below the permanent thermocline (Allen and Sanders 1996a). Recently, Benaim and Absalão (2011a, b, c) increased the number of protobranchiate Pelecypoda known in Brazilian waters by approximately 27%.

*Ledella* Verrill and Bush, 1897 is a genus that has a complex taxonomic history, including changes of the type species (Warén 1978, 1981, ICZN 1985, Allen and Hanna 1989). Information about this group in Brazilian waters is currently lacking. The most recent Brazilian catalogue of mollusks (Rios 2009) listed only *Ledella solidula* (Smith, 1885)and *Ledella semen* (Smith, 1885), with the latter given under the generic name of *Nuculana* Link, 1807. This does not reflect the present knowledge of this genus in Brazil. Five species of *Ledella* are currently known to be present in Brazilian waters: *L.semen* and *L. solidula*, as reported by Smith (1885); *Ledella ultima* (Smith, 1885) and *Ledella orixa* (Dall, 1927), as reported by Allen and Hanna (1989); and *Ledella acinula* (Dall, 1889), as reported by Allen and Sanders (1996b).

Recently, Sharma *et al.* (2013) completed a major molecular analysis of the Protobranchia, showing that the genus *Ledella* is not monophyletic. However, for the use of species delimitation, we have analyzed all the species here described as a unit.

Like the majority of protobranchiate Pelecypoda, *Ledella* has a conservative shell shape, subtle interspecific differences and a lack of clear boundaries between genera. The species within this genus form groups or clusters with conchological similarity, as occurs in *Yoldiella* Verrill and Bush, 1897(La Perna 2004, Benaim and Absalão 2011a). The species presented in this paper are no exception to this rule, and due to their similar shell outline, a morphometric analysis was required to corroborate their delimitation into different species. Therefore, this paper contributes to the knowledge of the genus *Ledella* from Brazil by describing four previously unknown species together with their morphometric data.

## MATERIAL AND METHODS

The samples used in the study were collected during three projects. First, the "Live Resources of the Economic Exclusive Zone" (Revizee) project, which took place during 2001 (Table S1) and was sponsored by the Brazilian government as part of international demands to retain Brazilian authority over the 200 miles of territorial sea. This project extended across the Brazilian continental margin and the methodological details are given in Amaral and Rossi-Wongtschowski (2004) and Lavrado and Ignacio (2006). Second, the "Environmental

Characterization of Campos Basin, RJ, Brazil" (Oceanprof) project, which was conducted during the years 2002 and 2003 (Table S1). Finally, "Habitats Project – Campos Basin Environmental Heterogeneity", which was developed during 2008 and 2009 (Table S2). The two latter projects were sponsored directly by Petrobras and were carried out using the research vessel *Astro–Garoupa* equipped with a box corer. Details about the associated methodological procedures can be found in Lavrado and Brasil (2010). All biological material was sorted under magnification and the best-preserved specimens of each species were examined and photographed under a scanning electron microscope (ZEISS EVO 40) at the Gerência de Bioestratigrafia e Paleoecologia Aplicada (BPA) of the Petrobras Research Center (Centro de Pesquisas da Petrobras – CENPES). Live-collected specimens were very common in the material obtained from the Habitats Project, which constituted most of the examined material. All of the shells from the Revizee and Oceanprof projects were empty. The specimens studied have been deposited primarily in the mollusk collection of the Instituto de Biologia, Universidade Federal do Rio de Janeiro (IBUFRJ), and secondarily at the Museu Nacional do Rio de Janeiro (MNRJ), the Museu Oceanográfico Eliézer de Carvalho Rios, Universidade Federal do Rio Grande (MOFURG), and the Muséum national d'Histoire naturelle (MNHN), Paris.

All of the *Ledella* samples studied here were first designated as morphospecies. We conducted an exploratory analysis based on the Population Aggregation Analysis (Davis and Nixon 1992) using1362 valves and taking into account the "traditional" criteria used in bivalve taxonomy (Cox 1969, Bailey 2009, Killeen and Turner 2009), which are based on conchological characters. The identifications were made through comparisons with figures of the type species and descriptions available in the literature (Smith 1885, Laghi 1984, Allen and Hanna 1989, Laghi and Palazzi 1989, La Perna 2004,Rios 2009,Allen and Sanders 1996b).

Morphological orientation in pelecypods is usually related to a series of axes (Bailey 2009). To determine dorsal and ventral height (DH and VH, respectively), we used the antero-posterior orientation based on an imaginary line passing under the adductor muscles scars, which divides the body into dorsal and ventral areas (Allen 1985).

**Measurements**

Considering the inequivalve condition of these species, the valves were separated to obtain measurements of both left and right valves. Whenever possible, the valves measured came from the same individual. This was not always feasible because the measurements of the hinge teeth require that they are well-preserved.

The valves were photographed, together with a scale, using a Canon Power Shot G10 camera attached to a Zeiss Stemi SV11 stereomicroscope. The photographs were then analyzed to obtain the measurements, using the software Axio Vision release 4.6.3 (4.2007). To ensure the valves were parallel to the plane of the camera lens, a platform made of playdough was used.

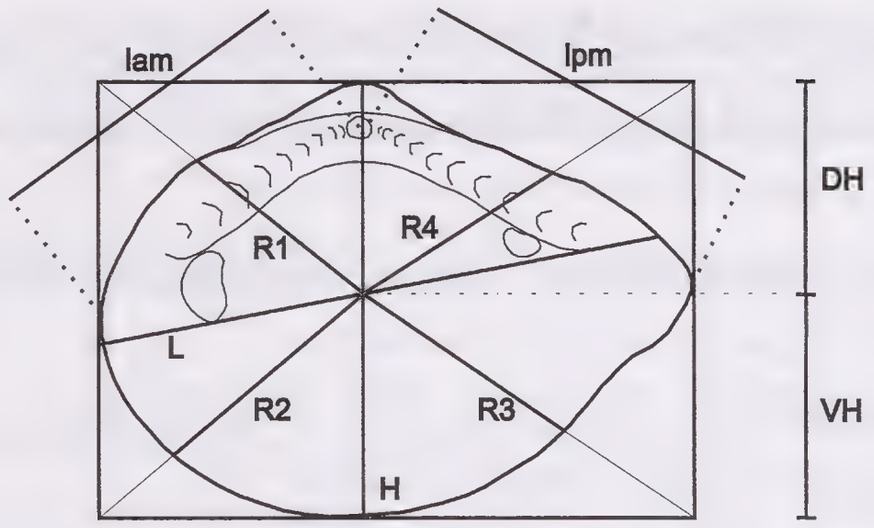


**Figure 1.** Measurement scheme for the general shell shape. Total length and height (L and H, respectively); dorsal and ventral height (DH and VH, respectively); length of the antero and postero-dorsal margin (lam and lpm, respectively); and lengths of the four lines beginning near the shell center and radiating toward the four corners of the rectangle delimiting the shell (R1, R2, R3, and R4).

Measurements representing the general shell shape were taken as follows: total length (L); total height (H); dorsal height (DH); ventral height (VH); length of the antero-dorsal margin (lam); length of the postero-dorsal margin (lpm); and lengths of the four lines beginning near the shell center and radiating toward the four corners of the rectangle delimiting the shell (R1, R2, R3, and R4) (Fig.1). Similar approaches were used by Knudsen (1970), Rabarts and Whybrow (1979), Warén (1989), Rhind and Allen (1992), Allen *et al.* (1995), Bonfitto and Sabelli (1995), Fuiman *et al.* (1999), Benaim and Absalão (2011b), and Benaim *et al.* (2011).

The measurements taken for the hinge plate were as follows: length of the anterior and posterior parts of the hinge plate (ahp and php, respectively); width of the anterior part of the hinge plate and its teeth (wap and wat, respectively); and width of the posterior part of the hinge plate and its teeth (wpp and wpt, respectively), as previously conducted by Benaim and Absalão (2011b). Furthermore, ten additional measurements were taken with the valves in dorsal view, replicating the method of Benaim *et al.* (2011): width of the valve (W); total length of the hinge plate (lhp); dorsal length of the anterior and posterior parts of the hinge plate (dahp and dphp, respectively); height of the highest tooth of the anterior and posterior parts of the hinge plate (hat and hpt, respectively); and lengths between the center of the highest tooth of the anterior and posterior parts of the hinge plate to the umbo (alu and plu, respectively) and to the respective margins of the valve (alm and plm, respectively) (Fig.2). These hinge plate measurements taken in the dorsal view have been used only once previously, by Benaim *et al.* (2011) on the genus *Yoldiella*.

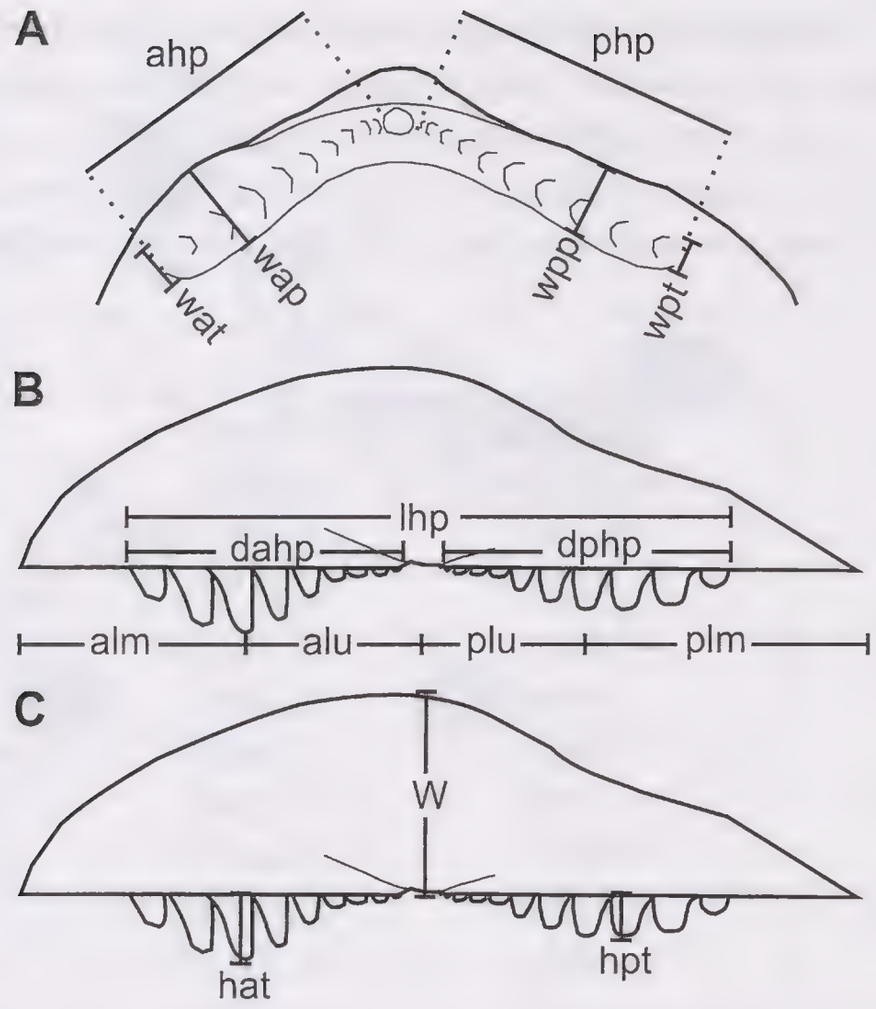


**Figure 2.** Measurement scheme for the hinge plate and width of the valve. **A,** length of the anterior and posterior parts of the hinge plate (ahp and php, respectively); width of anterior part of the hinge plate and teeth (wap and wat, respectively); and width of the posterior part of the hinge plate and teeth (wpp and wpt, respectively). **B,** total length of the hinge plate (lhp); dorsal length of the anterior and posterior parts of the hinge plate (dahp and dphp, respectively); and lengths between the center of the highest tooth of the anterior and posterior parts of the hinge plate to the umbo (alu and plu, respectively) and to the respective margins of the valve (alm and plm, respectively). **C,** width of the valve (W); and height of the highest tooth of the anterior and posterior parts of the hinge plate (hat and hpt, respectively).

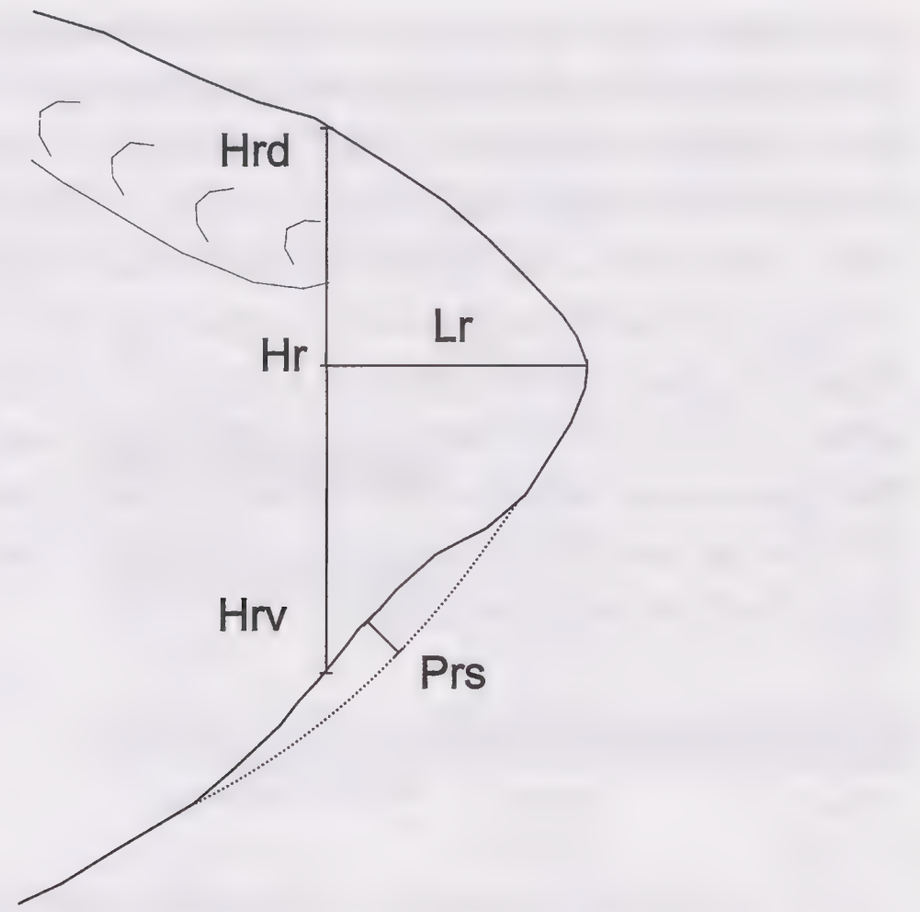


**Figure 3.** Measurement scheme for the shape of the rostrum. Height of the rostrum (Hr); length of the rostrum (Lr); dorsal and ventral heights of the rostrum (Hrd and Hrv, respectively); and profundity of the rostrum's sinuosity (Prs).

An additional set of five measurements was implemented in this study: height of the rostrum (Hr), measured by a line that borders the first tooth of the posterior hinge plate and goes straight from the dorsal to the ventral margins of the valve; length of the rostrum (Lr), measured perpendicularly from the Hr line to the edge of the rostrum; dorsal and ventral heights of the rostrum (Hrd and Hrv, respectively), using the Lr line to divide the dorsal and ventral regions of the rostrum; and profundity of the rostrum's sinuosity (Prs), which is the greatest linear distance from the lower point of the sinuosity to the imaginary line of continuity of the valve (Fig. 3).

We also calculated 22 ratios: ahp/lam, alm/plm, alu/alm, dahp/dphp, H/L, hat/dahp, hat/hpt, hat/W, hpt/dphp, hpt/W, Hr/Lr, Hr/H, Hrd/Hrv, lhp/L, Lr/L, Lr/plm, php/lpm, plu/plm, W/L, W/lhp, wap/ahp and wpp/php.

**Morphometric analyses**

One could argue that the above ratios will inevitably be strongly correlated with the variables that were utilized in the calculation of these ratios, leading to redundancy in the analysis. To avoid this problem, in addition to redundancy between the variables themselves, we performed a preliminary correlation analysis among all variables and excluded one of each pair of values with strong correlation ($r \geq 0.9$). The normality of variables was verified through normal probability plots and, when necessary, appropriate transformations were implemented to normalize the data.

Discriminant function analysis was used to determine if these morphospecies could be objectively identified through the defined variables and, if so, which of the analyzed features were the most important for their discrimination. Forward stepwise procedures were employed to select the most useful discriminating variables. To perform these analyses, we standardized the morphometric data as described by Romesburg (1984). All statistical procedures were performed using STATISTICA software (version 7.0), StatSoft, Inc., Tulsa, Oklahoma.

The analyses were conducted for two separate subgroups: the right valves and the left valves. Taking into account the inequivalve condition of these species, a joint analysis would not have provided information about which group of valves could determine the morphospecies more accurately nor about the features of each valve which are the most important for morphospecies discrimination.

**Taxonomic Discussion**

Each morphospecies considered in this study was first compared with the co-generic species previously reported in Brazilian waters. They were then compared with the co-generic species that have similar shell shapes and, finally, with the other morphospecies described in this work.

Only Recent species were used to discuss the new species described herein. Thus, somewhat similar species such as *Ledella peraffinis* (Seguenza, 1877) (Miocene), whose neotype was figured by Laghi and Palazzi (1989), *Ledella pusio* (Philippi, 1844) (Pliocene), which was reviewed and figured by Laghi (1984), and *Ledella seminulum* (Seguenza, 1877) (Pleistocene-Pliocene) and *Ledella nicotrae* (Seguenza, 1877) (Pliocene), both figured by La Perna *et al.* (2004), were not considered in the discussion. Besides the chronological distance between the Recent and fossil species, all of these fossil species are from the Mediterranean Sea.

## RESULTS

A traditional taxonomic descriptive approach suggested the existence of four morphospecies which provided the base for the morphometric procedures.

### Right Valves

For this analysis, only nine variables were excluded due to strong correlation with the other variables. The excluded variables were: L, H, DH, lam, php, R2, R3, R4 and lhp. The remaining 44 variables were included in the analysis and 25 of them were retained in the final model, which was in 95% agreement with the traditional criteria (Table 1).

This rate of agreement was achieved using three discriminant functions (df). The first one (df1) represents the role of the shape of the Rostrum (Prs, Lr and Lr/plm) in the discrimination. Df2 represents the joint role of the Rostrum Height (Hrd e Hrd/Hrv) and Hinge Plate Width (wap and wpp) in the discrimination. Df3 represents the role of the Hinge Plate (hpt, wap/ahp, wap and hpt/W) in the discrimination. These three roles were also perceived during the traditional and more intuitive taxonomic discrimination of the individuals.

Three variables (ahp/lam, H/L and wpt) made a relatively small contribution to the model, but we decided to retain them because excluding them from the analysis generated a model with only 14 variables and 86.66% agreement with the traditional criteria, which is 8.34% lower than the first result.

### Left Valves

For this analysis, only nine variables were excluded due to strong correlation with the others. These variables were: L, H, DH, lam, php, R3, R4, lhp and hpt. The remaining 44 variables were included in the analysis and 24 of these were retained in the final model, which showed 88.33% agreements with the traditional criteria (Table 2), 6.67% less than the result obtained for the right valves.

This rate of agreement was achieved using three discriminant functions. The first one (df1) represents the roles of the width of the valve (W) and of the distance of the highest tooth of the anterior part of the hinge plate to its respective margin (alm); df2 represents the role of the expansion of the antero-ventral region of the valve (R2) in the discrimination; df3 represents the role of the ratio between the size of the highest tooth of the posterior part of the hinge plate and the width of the valve (hpt/W) in the discrimination. In addition, in all three functions the ratio between the width of the valve and its length (W/L) was one of the two main variables: the ratio between the dorsal length of the hinge plate and the length of the valve (lhp/L) was one of the main variables in df1 and one of the two main variables in df2 and df3, and the ratio between the width of the valve and the dorsal length of the hinge plate (W/lhp) was one of the two main variables in df2 and df3. The presence of these variables in more than one discriminant function reinforces the importance of the width of the valve, the length of the hinge plate and the length of the valve to the discrimination of the morphospecies. The prominence of these variables in the

**Table 1.** Standardized coefficients for canonical variables for the right valves analysis. The most relevant variables in each axis are marked in dark gray; the second most representative variables in each axis are marked in light gray. The variables which made minor contributions are marked in italics. Df, discriminant function.

| | Df1 | Df2 | Df3 |
|---|---|---|---|
| Prs | 0.84685 | 0.57349 | 0.08940 |
| W | 0.40454 | 0.14923 | 1.79748 |
| *ahp/lam* | *-0.34177* | *0.51987* | *0.54561* |
| lhp/L | 0.75184 | -0.27905 | 0.44486 |
| Plu | -0.48379 | 0.59059 | 0.82643 |
| Alm | 0.59928 | -0.29880 | 2.74110 |
| Hr/Lr | -0.98651 | -1.26410 | -0.70248 |
| Ahp | 0.20366 | 0.22406 | -2.66803 |
| *H/L* | *0.36787* | *-0.48827* | *-0.05886* |
| hat/dahp | 0.62724 | 0.05129 | 0.82733 |
| Alu | 0.26413 | -0.56459 | 0.05034 |
| Hat | -1.01679 | 0.29528 | -0.27112 |
| Lpm | 0.74758 | -0.52086 | -0.45604 |
| Hrd | 0.34414 | 2.25031 | 0.70813 |
| alm/plm | -0.59847 | 0.09829 | -2.33328 |
| Hrd/Hrv | -0.70831 | -1.84689 | -0.70744 |
| Lr | -1.73270 | -1.34534 | -2.74996 |
| Hpt | -1.16240 | 0.20600 | -3.62005 |
| *Wpt* | *0.44496* | *-0.28454* | *0.51637* |
| Wpp | -0.36244 | 0.81991 | -0.11739 |
| Wat | -0.02904 | 0.70197 | -0.09151 |
| wap/ahp | -0.35423 | 0.75593 | -4.37649 |
| Lr/plm | 1.04844 | -0.61189 | 2.15145 |
| Wap | 0.54872 | -1.48020 | 4.63718 |
| hpt/W | 0.61434 | -0.61345 | 2.37309 |
| Eigenval | 3.70612 | 1.51830 | 1.05303 |
| Cum.Prop | 0.59039 | 0.83225 | 1.00000 |

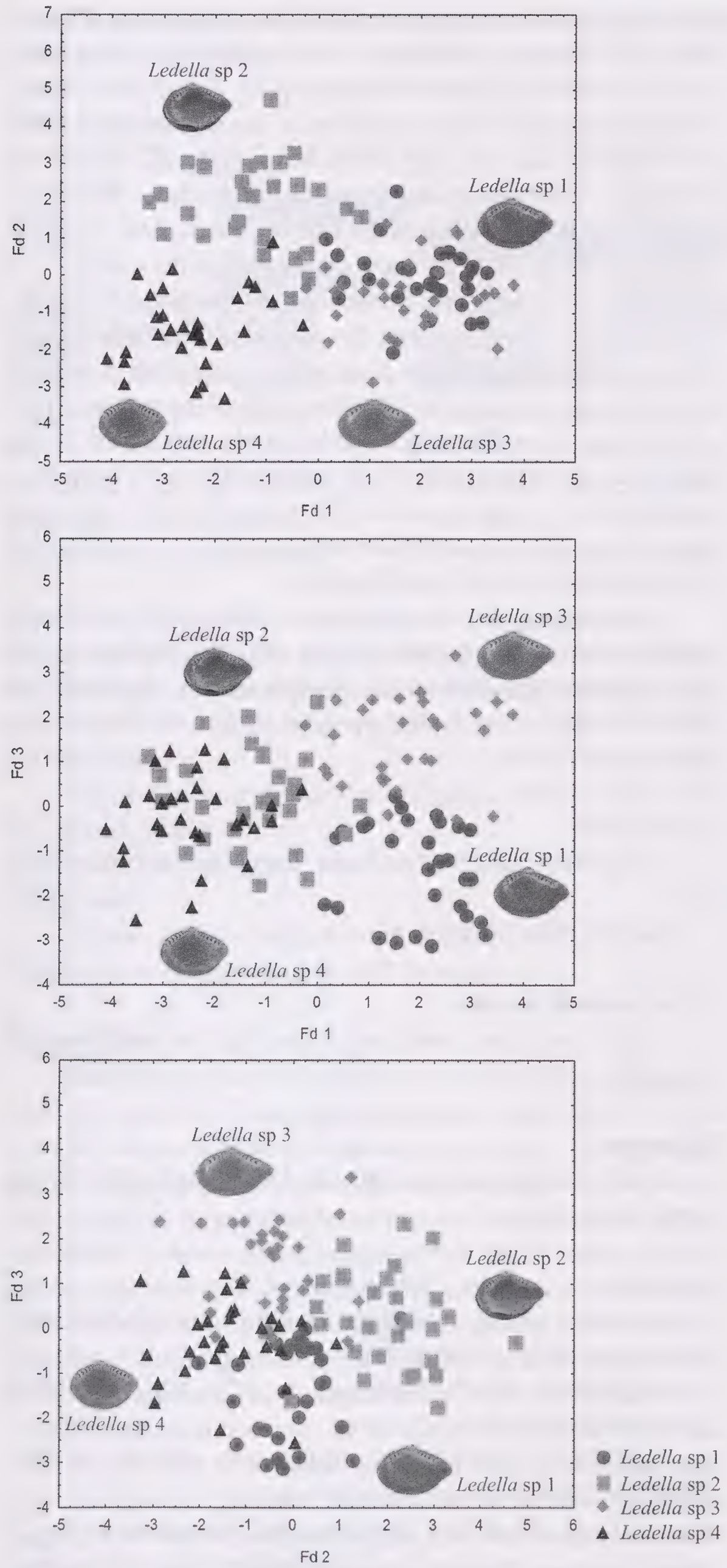


**Figure 4.** Canonical analysis scatterplots for the right valves, combining all three discriminant functions (df).

three discriminant functions shows the importance of the hinge plate and the width and length of the valve in this analysis, in contrast to the results of the right valve analysis,

**Table 2.** Standardized coefficients for canonical variables for the left valves analysis. The most relevant variables in each axis are marked in dark gray; the second most relevant variables in each axis are marked in light gray. The variables that made minor contributions are marked in italics. Df, discriminant function.

| | Df1 | Df2 | Df3 |
|---|---|---|---|
| Hr/Lr | 1.216731 | 0.33400 | -0.42661 |
| W | -0.807000 | -1.69353 | 0.66830 |
| H/L | -0.732078 | 0.54540 | -1.49951 |
| alm | 1.332459 | 0.10327 | -0.65290 |
| *php/lpm* | *-0.274477* | *0.00366* | *0.09067* |
| *ahp/lam* | *0.060819* | *-0.33352* | *-0.18710* |
| lhp/L | -0.801864 | -7.11341 | -7.70510 |
| Lpm | -0.098203 | 1.17700 | -0.46356 |
| wpt | -0.226754 | 0.42273 | 0.91259 |
| ahp | 0.661153 | 1.17329 | 1.74951 |
| R1 | -0.193882 | -1.79420 | 0.91022 |
| *Prs* | *-0.292743* | *-0.40283* | *0.10688* |
| *hat/hpt* | *0.286672* | *0.15125* | *-0.35170* |
| W/L | 1.921255 | 10.84032 | 13.32499 |
| W/lhp | -0.658799 | -6.81776 | -6.09872 |
| alu | -0.755089 | 1.14047 | 1.01010 |
| R2 | 0.829580 | 1.d64855 | -1.60351 |
| VH | -0.474442 | -1.70245 | 2.36178 |
| hpt/W | -0.125905 | 0.60649 | 4.35272 |
| hpt/dphp | 0.102861 | -0.25046 | -3.73286 |
| alu/alm | 1.292262 | -1.03185 | -1.65989 |
| dphp | 0.125179 | -0.81548 | -4.69959 |
| *wpp* | *-0.150277* | *-0.42347* | *-0.34195* |
| *wat* | *0.430124* | *0.29482* | *-0.07997* |
| Eigenval | 2.318400 | 1.96972 | 0.66221 |
| Cum.Prop | 0.468332 | 0.86623 | 1.00000 |

in which the shape of the rostrum was important to the discrimination whilst the width and length of the valve were only minor contributors.

Six variables (php/lpm, ahp/lam, Prs, hat/hpt, php and dahp) made relatively small contributions to the model, but we again decided to retain these, in accordance with the first analysis. Removing these variables from the analysis generated a model with 18 variables and with 82.5% of the cases in agreement with the traditional criteria, which is 5.83% lower than the first result.

**Hinge Plate**

We also decided to test the discriminatory power using the hinge plate features alone, following Benaim *et al.* (2011). The analyses were again performed using the right and left valves in separate subgroups, and in both cases, nine variables were included in the model. For the right and left valves respectively, the models showed 66.66% and 64.16% agreement with the traditional criteria (Table 3).

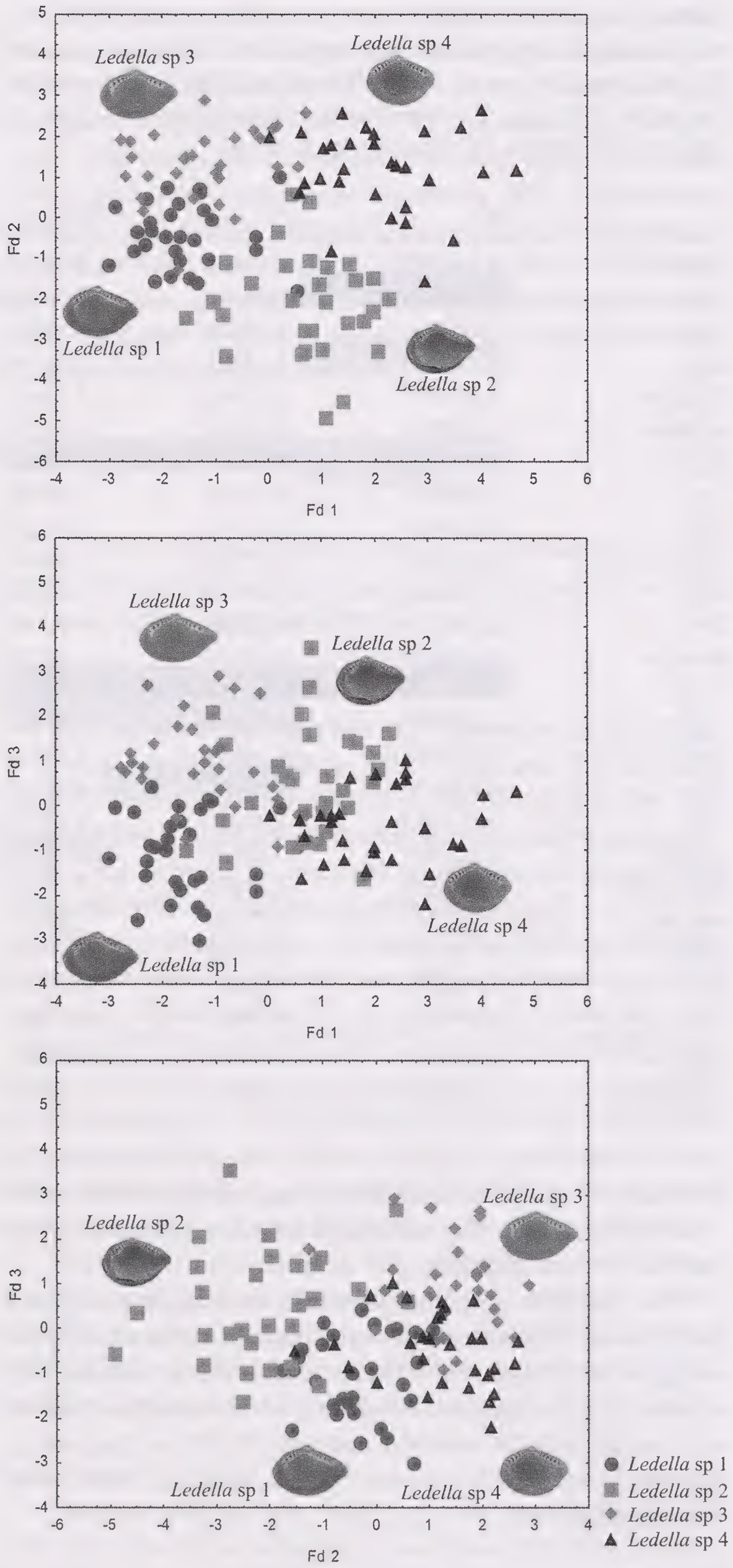


**Figure 5.** Canonical analysis scatterplots for the left valves, combining all three discriminant functions (df).

These rates of success were achieved using three discriminant functions (df) for each analysis. For the right valves analysis, the first one (df1) represents the tridimensional shape of the anterior part of the hinge plate; df2 represents the thickness of the posterior part of the hinge plate; df3 represents the relative positions of the highest teeth from anterior and posterior parts of the hinge plate. For the left valves, df1 represents the relative positions of the highest teeth from anterior and posterior parts of the hinge plate; df2 represents the shape of the posterior part of the hinge plate; df3 represents the relative position of the highest tooth of the anterior part of the hinge plate on the anterior part of the valve.

Only two variables were important in both hinge plate analyses: alm/plm, which indicates the position of the highest teeth of the anterior and posterior parts of the hinge plate in relation to the margin, and wpp, which is the width of the posterior part of the hinge plate. The first variable may be influenced by the antero-dorsal rostrum present in some of the morphospecies; however, this was not measured. The second variable had been perceived as an important character previously, during the initial discrimination of these morphospecies.

Considering the morphological differences previously detected during the initial analysis of the material and the high support provided by the morphometric approach for the distinction of our initial morphospecies, we describe the four species herein.

## Systematics

Order NUCULANIDA Carter, Campbell and Campbell, 2000

Family NUCULANIDAE

### *Ledella spocki* sp. nov.

(Figs. 4 and 5 as *Ledella* sp. 1 and Fig. 6 as *Ledella spocki* sp. nov.)

### Holotype

MNRJ 30480, Habitats 7 #F6 R2, 08-VII-2008. 22°19′11″S; 40°05′44″W; 403m.

### Paratypes

IBUFRJ 19238, Habitats 7 #H6 R2, 07-VII-2008. 21°44′21″S; 40°05′18″W; 402 m.

MOFURG 51797, Habitats 8 #C6 R3, 31-I-2009. 22°59′00″S; 40°48′28″W; 376.6 m.

MNHN IM-2010-21015, Habitats 7 #B6 R2, 04-VII-2008. 23°12′31″S; 40°58′31″W; 447.4m.

**Material examined** (See supplemental document at: http://www.bioone.org/doi/suppl/10.4003/006.032.0201/suppl_file/Viegas_2014_Suppl_docs.pdf)

### Etymology

This species is named after the fictional character "Spock" from the Star Trek TV and movie series. The overall shape of its valves resembles the shape of the pointed ear of the Vulcans, a humanoid extraterrestrial species depicted in

**Table 3.** Standardized coefficients for canonical variables for the hinge plate analyses. The most relevant variables are marked in gray. Df, discriminant function.

| Right Valves | | | | Left Valves | | | |
|---|---|---|---|---|---|---|---|
| | df1 | df2 | df3 | | df1 | df2 | df3 |
| Hat | -0.717286 | -0.292718 | -0.74520 | dphp | -1.01472 | 0.921452 | 0.37551 |
| alm/plm | -0.080687 | -0.894922 | -1.46122 | alm/plm | -1.51834 | 0.427152 | 0.84545 |
| wap/ahp | 0.843338 | 0.364217 | -0.98901 | ahp | -1.04440 | 0.109696 | -0.40674 |
| plu/plm | -0.476898 | 0.052819 | 1.15000 | alu/alm | -0.61262 | 0.470459 | 0.95693 |
| alu/alm | 0.199852 | -0.538310 | -1.10171 | plu | 0.79939 | -0.198373 | -0.41296 |
| wpp | -0.020109 | 1.016999 | -0.13674 | wpp | 1.58973 | 0.734929 | 0.80325 |
| wpp/php | -0.474712 | -0.401955 | -0.05389 | wpt | -0.36763 | -0.690460 | -1.17862 |
| wpt | 0.034626 | -0.873887 | 0.55696 | wpp/php | -0.85653 | -0.017427 | 0.02813 |
| wat | -0.443634 | 0.447644 | -0.00058 | hat/dahp | -0.36750 | 0.072022 | 0.24557 |
| Eigenval | 0.848731 | 0.477082 | 0.11853 | Eigenval | 0.98125 | 0.626145 | 0.09994 |
| Cum.Prop | 0.587624 | 0.917935 | 1.00000 | Cum.Prop | 0.57473 | 0.941466 | 1.00000 |

this series. Because "Mr. Spock" is the most famous Vulcan in the series, the species has been named after him.

**Distribution**

Only known from the Campos Basin, off the coast of Rio de Janeiro, Brazil.

**Diagnosis**

Thin shell with marked anterior and posterior shoulders. Acute rostrum. Profound rostral sinuosity.

**Description**

Shell oblong–elliptical, inflated, thin, inequivalve, inequilateral, H/L about 0.72; umbones prominent, opisthogyrous and inwardly directed. Antero-dorsal margin convex; anterior margin showing a shoulder. Rounded ventral margin forming a sinuosity leading to an acute rostrate posterior end which points downward; postero-dorsal margin almost straight, with a shoulder near the end of the hinge plate. Smooth outer surface. Hinge plate interrupted by a small and almost rounded resilifer. Posterior part of the hinge plate longer and thinner than anterior one in adult specimens, and almost equal in juveniles. Width of the anterior and posterior rows of teeth occupying about 60% and 58%, respectively, of the total width of the hinge plate of the right valves and about 59% and 55% of the anterior and posterior hinge plates, respectively, of the left valve. Shell microsculpture: the prodissoconch presents a weak granulation and the hinge teeth present pustules on the side that faces the umbones. Maximum shell length: 1.94 mm. Prodissoconch height: 70μm. Prodissoconch length: 73μm. (Table 4)

**Remarks**

*Ledella spocki* sp. nov. is similar to *L.semen* with respect to the general shell shape and in the acuteness of its rostrum, but they can be distinguished on the basis of the less opisthogyrous umbones and the more profound rostral sinuosity of *L. spocki* sp. nov.

*Ledella spocki* sp. nov. shares a long and acute rostrum and a profound rostral sinuosity with *L. solidula*, but *L. spocki* sp. nov. can be distinguished from the latter on the basis of having no concentric lines and a rostrum that is shorter and less downward-pointing than that of *L. solidula.*

*Ledella spocki* sp. nov. differs from *L. ultima* in that the former has no concentric lines and presents thinner teeth on the hinge plate and a more acute rostrum than *L. ultima.*

*Ledella spocki* sp. nov. differs from *L. acinula* in that the former has no concentric lines and presents a more acute rostrum and a less inflated posterior region of the shell than *L. acinula.*

*Ledella spocki* sp. nov. differs from *L. orixa* in that the former presents less opisthogyrous umbones, a larger posterior region in comparison to the anterior region and a smaller anterior part of the hinge plate when compared to the posterior part.

*Ledella spocki* sp. nov. can be distinguished from *L. acuminata* (Jeffreys, 1870) in that the former has no concentric lines, a shorter hinge plate and presents thinner hinge teeth in relation to the hinge plate thickness, compared with *L. acuminata.*

***Ledella legionaria* sp. nov.**

(Figs. 4 and 5 as *Ledella* sp. 2 and Fig. 7 as *Ledella legionaria* sp. nov.)

**Holotype**

MNRJ 30481, Habitats 7 #F6 R2, 08-VII-2008. 22°19′11″S; 40°05′44″W; 403m.

**Paratypes**

IBUFRJ19300, Habitats 9 #H6 R2, 05-II-2009. 21°44′21″S; 40°04′53″W; 404 m.

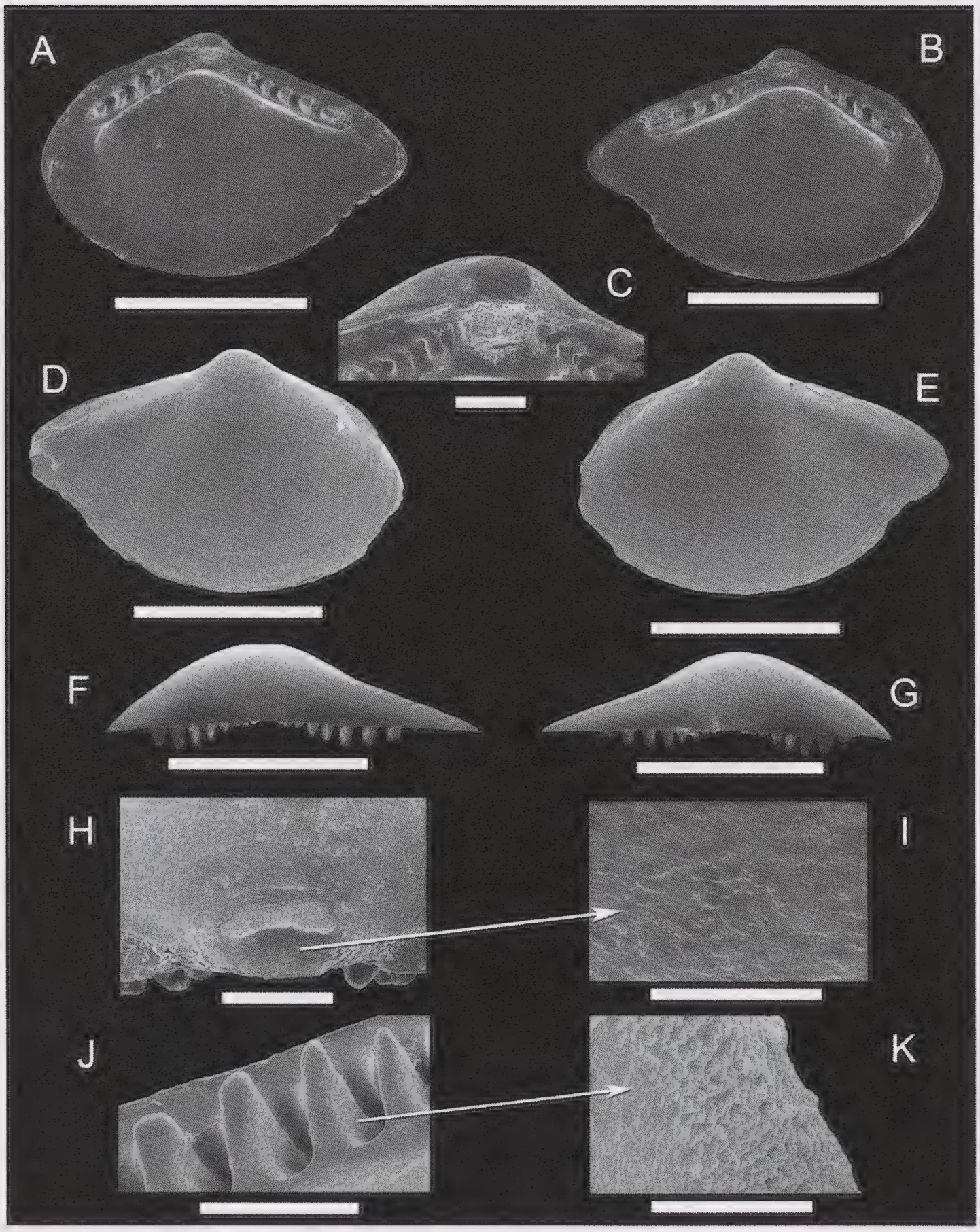


**Figure 6.** *Ledella spocki* sp. nov. (Holotype MNRJ 30480). Internal view: **A,** right valve; **B,** left valve. External view: **D,** right valve; **E,** left valve. Dorsal view: **F,** right valve; **G,** left valve. Details: **C,** resilifer of the right valve. Prodissoconch (IBUFRJ 19239): **H,** overview; **I,** detail of the tip of the prodissoconch showing some granulation. Hinge teeth (IBUFRJ 19247): **J,** overview; **K,** detail of the tooth showing the tooth pustules. Scales A, B, D–G: 1mm. C, H: 0.1mm.I: 0.01 mm. J: 0.2 mm. K: 0.02 mm.

MOFURG 51798, Habitats 7 #F6 R1, 08-VII-2008. 22°19′10″S; 40°05′42″W; 402.3m.

MNHN IM-2010-21016, Revizee V #41, 20-VII-2001. 21°13′S; 40°13′W; 1000m.

**Material examined** (See supplemental document at: http://www.bioone.org/doi/suppl/10.4003/006.032.0201/suppl_file/Viegas_2014_Suppl_docs.pdf)

**Etymology**

This species is named after the Roman legionnaires. The shape of its rostrum resembles the outline of a shoulder armor, similar to those used by the legionaries in their *lorica segmentata* (segmented plates) armor. Additionally, its shell is thicker than those of the other species described herein, as though the animal wears a heavier armor than the others.

**Distribution**

Only known from the Campos Basin, Rio de Janeiro, Brazil.

**Diagnosis**

Shell thick with prominent anterior and posterior shoulders. Rostrum acutely rounded. Profound rostral sinuosity, more profound in the left valve than in the right one.

**Description**

Shell oblong–elliptical, inflated, thick, inequivalve, inequilateral, H/L about 0.74; umbones prominent, opisthogyrous and inwardly directed. Antero-dorsal margin convex, acute shoulder delimiting antero-dorsal and anterior margins, merging to a convex ventral margin. Ventral margin forming a sinuosity leading to a rostrate posterior end which points slightly downward; postero-dorsal margin almost straight, with a marked shoulder near the end of the hinge plate. Hinge plate interrupted by a deep, rounded resilifer. Posterior part of the hinge plate longer and thinner than anterior one in adult specimens, and almost equal in juveniles. Width of the anterior and posterior rows of teeth occupying about 61% and 56%, respectively, of the total width of the hinge plate on the right valves and about 61% and 57% to the anterior and posterior parts of the hinge plates, respectively, on the left valve. Shell microsculpture: the prodissoconch presents a weak granulation and the hinge teeth present pustules on the side that faces the umbones. Maximum shell length: 2.31 mm. Prodissoconch height: 77 μm, length: 86 μm. (Table 4)

**Remarks**

*Ledella legionaria* sp. nov. differs from *L.semen* in having less opisthogyrous umbones, a more profound rostral sinuosity and a less acute rostrum than *L. semen*.

*Ledella legionaria* sp. nov. differs from *L. solidula* in having no concentric lines and in presenting a prominent shoulder in the antero-dorsal region and a rostrum that is shorter and less acute than that of *L. solidula*.

*Ledella legionaria* sp. nov. differs from *L. ultima* in having no concentric lines and in presenting thinner teeth on the hinge plate and a more acute rostrum than *L. ultima*.

*Ledella legionaria* sp. nov. differs from *L. acinula* in having no concentric lines and in presenting a more acute rostrum and a less inflated posterior region of the shell than *L. acinula*.

*Ledella legionaria* sp. nov. differs from *L. orixa* in presenting less opisthogyrous umbones, a larger posterior region than the anterior region and a smaller anterior part of the hinge plate in comparison to the posterior part.

Compared to *Ledella sublevis* Verrill and Bush, 1898, *L. legionaria* sp. nov. has a similar shell shape, but a less smooth postero-dorsal margin and a longer posterior part of the hinge plate when compared to the anterior part, with thinner hinge teeth than *L. sublevis*.

Compared to *Ledella jamesi* Allen and Hanna, 1989, *L. legionaria* sp. nov. has a similar shell shape, with a shoulder on the postero-dorsal margin, but *L. legionaria* sp. nov. has a longer rostrum and no concentric lines.

*Ledella lusitanensis* Allen and Hanna, 1989, also has a similar shell shape when compared to *L. legionaria* sp. nov., but the latter has a shoulder in the postero-dorsal margin and a more inequilateral hinge plate, with the posterior part of the hinge plate longer and with thinner teeth than the anterior one.

Compared to *Ledella spocki* sp. nov., *L. legionaria* sp. nov. is larger, thicker, more inflated and has a less profound rostrum sinuosity on the right valve. *Ledella legionaria* sp. nov. also has a shorter rostrum and a more prominent posterior shoulder. *Ledella legionaria* sp. nov. has longer posterior parts of the hinge plate on both valves, but longer anterior parts of the hinge plate are present only on the right valve. These species do not vary much from each other with respect to the thickness of the hinge plate or that of the hinge teeth. Regarding the prodissoconch, they do not differ much in height and microsculpture, but the prodissoconch of *L. legionaria* sp. nov. is longer in length than the prodissoconch of *L.spocki* sp. nov.

### *Ledella elfica* sp. nov.

(Figs. 4 and 5 as *Ledella* sp. 3 and Fig. 8 as *Ledella elfica* sp. nov.)

**Holotype**

MNRJ 30482, Habitats 7 #H6 R2, 07-VII-2008. 21°44′21″S; 40°05′18″W; 402m.

**Paratypes**

IBUFRJ 19371, Habitats 7 #H6 R1, 06-VII-2008. 21°42′02″S; 40°06′15′W; 404.7 m.

MOFURG 51799, Revizee Central V #52, 21-VII-2001. 21°46′S; 40°05″W; 450 m.

MNHN IM-2010-21017, Habitats 7 #F6 R2, 08-VII-2008. 22°19′11″S; 40°05′44″W; 403m.

**Material examined** (See supplemental document at: http://www.bioone.org/doi/suppl/10.4003/006.032.0201/suppl_file/Viegas_2014_Suppl_docs.pdf)

**Etymology**

This species is similar in shape to the ear of an elf from Norse mythology, so we decided to name this species after those elves.

**Distribution**

Only known from the Campos Basin, Rio de Janeiro, Brazil.

**Diagnosis**

Thin shell with anterior and posterior shoulders usually absent; when present, shoulders not prominent. Acute rostrum. Profound rostral sinuosity.

**Description**

Shell oblong–elliptical, inflated, thin, inequivalve, inequilateral, H/L about 0.72; umbones prominent, opisthogyrous and inwardly directed. Antero-dorsal margin convex; anterior margin rounded, smoothly merging to the slightly convex ventral margin. Ventral margin forming a sinuosity leading to a rostrate posterior end which points downward; postero-dorsal margin almost straight, sometimes weakly sloping downward near the end of the hinge plate. Smooth surface. Hinge plate interrupted by a deep, rectangular resilifer. Posterior hinge plate longer and thinner than anterior one in adult specimens, and almost equal in juveniles. Width of the anterior and posterior rows of teeth occupying about 60% and 59%, respectively, of the total width of the hinge plate of the right valves and about 62% and 59% to the anterior and posterior hinge plates, respectively, of the left valve. Shell microsculpture: the prodissoconch presents a weak granulation and the hinge teeth present pustules on the side that faces the umbones. Maximum shell length: 1.86 mm. Prodissoconch height: 83 μm. Prodissoconch length: 104 μm.(Table 4)

**Remarks**

Compared to *Ledella semen*, *L. elfica* sp. nov. has a similar shell shape, with a smooth outline and an acute rostrum, but *L. elfica* sp. nov. has less opisthogyrous umbones and a more profound rostral sinuosity.

*Ledella elfica* sp. nov. is similar to *L. solidula* in that both have an acute rostrum and a profound rostral sinuosity, but they can be distinguished because *L. elfica* sp. nov. does not have concentric lines and its rostrum is shorter and points less downwards than that of *L. solidula*.

*Ledella elfica* sp. nov. differs from *L. ultima* in having no concentric lines and in presenting thinner teeth on the hinge plate and a more acute rostrum than *L. ultima*.

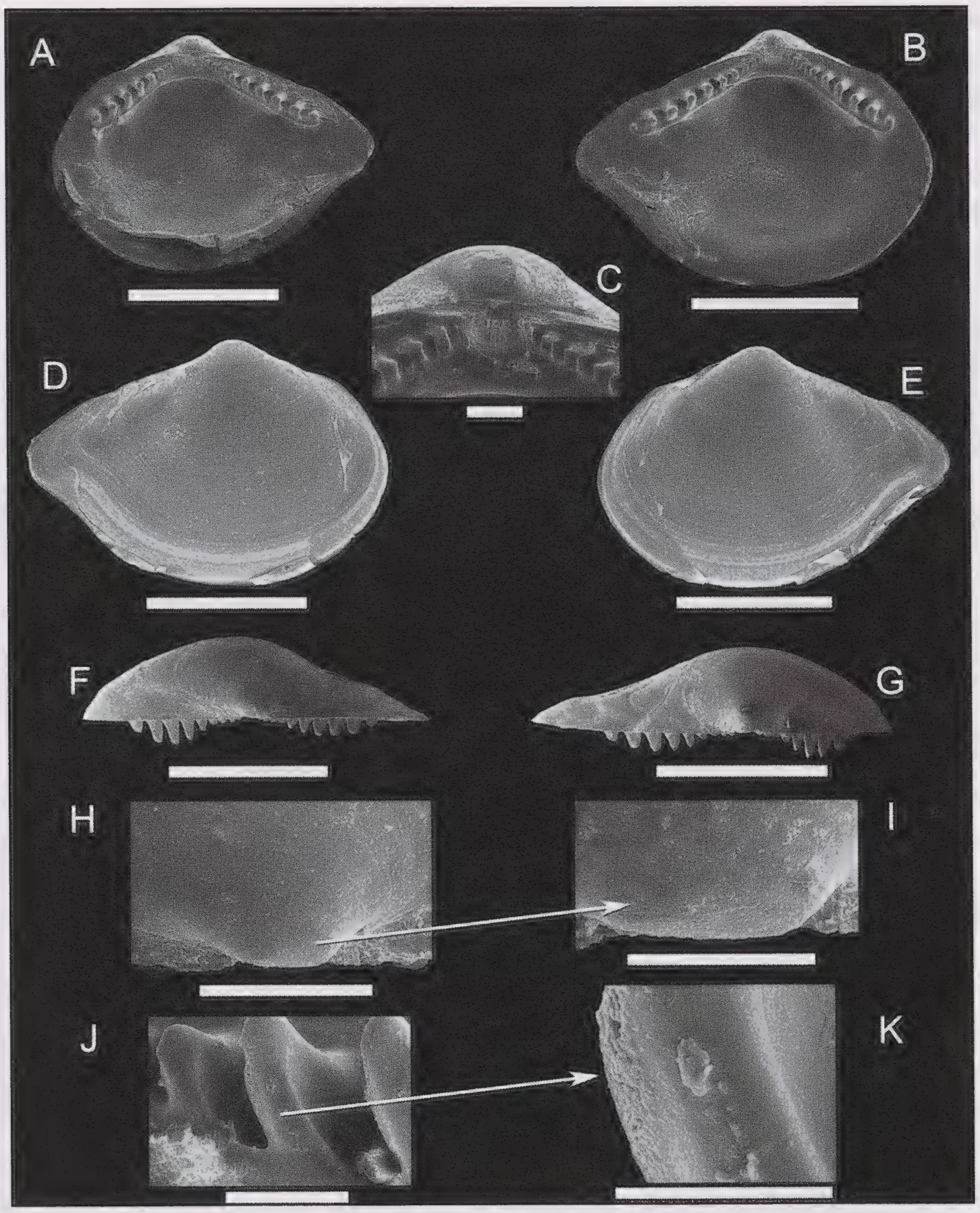


**Figure 7.** *Ledella legionaria* sp. nov. (Holotype MNRJ 30481). Internal view: **A,** right valve; **B,** left valve. External view: **D,** right valve; **E,** left valve. Dorsal view: **F,** right valve; **G,** left valve. Details: **C,** resilifer of the right valve. Prodissoconch (IBUFRJ 19284): **H,** overview; **I,** detail of the tip of the prodissoconch showing some granulation. Hinge teeth (IBUFRJ 14637): **J,** overview; **K,** detail of the tooth showing the tooth pustules. Scales A, B, D–G: 1 mm. C, H, J: 0.1 mm. I: 0.02 mm. K: 0.05 mm.

*Ledella elfica* sp. nov. differs from *L. acinula* in having no concentric lines and in presenting a more acute rostrum and a less inflated posterior region of the shell than *L. acinula.*

*Ledella elfica* sp. nov. differs from *L. orixa* in presenting less opisthogyrous umbones, a larger posterior region than the anterior region and a smaller anterior part of the hinge plate when compared to the posterior part.

*Ledella elfica* sp. nov. is similar to *L. acuminata* in the general outline of the shell, with an acute rostrum, a profound rostral sinuosity and the presence of a smooth shoulder on the postero-dorsal margin, which is found in some specimens of *L. elfica* sp. nov. However, *L. elfica* sp. nov. has no concentric lines, a shorter hinge plate and the hinge teeth occupy less of the hinge plate's width in comparison to *L. acuminata.*

*Ledella elfica* sp. nov. is similar to *L. spocki* sp. nov. in shape and thickness of the shell and in the length of the rostrum, but they can be distinguished because *L. elfica* sp. nov. is smaller in size (H, L and W), the anterior part of its hinge plate is thinner and longer on both valves and it has a less high and less acute rostrum with a less profound rostral sinuosity than *L. spocki* sp. nov. *Ledella elfica* sp. nov. also has a hinge plate (measured in dorsal view) that is longer in the right valve and shorter on the left one, compared to *L. spocki* sp. nov. Besides that, the hinge teeth of *L. elfica* sp. nov. are longer, in both valves, than those of *L. spocki* sp. nov. Regarding the prodissoconch, they do not differ much in height and microsculpture, but the prodissoconch of *L. elfica* sp. nov. is larger in length than the prodissoconch of *L.spocki* sp. nov.

*Ledella elfica* sp. nov. is similar to *L. legionaria* sp. nov. with respect to the general shell shape, but they can be distinguished because *L. elfica* sp. nov. has a longer and more acute rostrum than *L. legionaria* sp. nov. and its rostral sinuosity is more profound on the right valve and less profound on the left valve compared to *L. legionaria* sp. nov. With regard to the hinge plates, the hinge teeth of *L. elfica* sp. nov. occupy a larger part of the hinge plate thickness on the posterior part of the hinge plate than that of *L. legionaria* sp. nov. Regarding the prodissoconch, they do not differ much in height and microsculpture, but the prodissoconch of *L. elfica* sp. nov. is larger in length than the prodissoconch of *L. legionaria* sp. nov.

### *Ledella manati* sp. nov.

(Figs. 4 and 5 as *Ledella* sp. 4 and Fig. 9 as *Ledella manati* sp. nov.)

**Holotype**

MNRJ 30483, Revizee V #504, 02-VII-2001. 14°28′S; 38°54′W; 278m.

**Paratypes**

IBUFRJ 19398, Habitats 7 #C6 R1, 04-VII-2008. 22°59′00″S; 40°48′25″W; 387.4 m.

MOFURG 51800, Revizee Central V #1, 03-VII-2001. 13°04′S; 38°21′W; 450 m.

MNHN IM-2010-21018, Habitats 7 #F6 R2, 08-VII-2008. 22°19′11″S; 40°05′44″W; 403m.

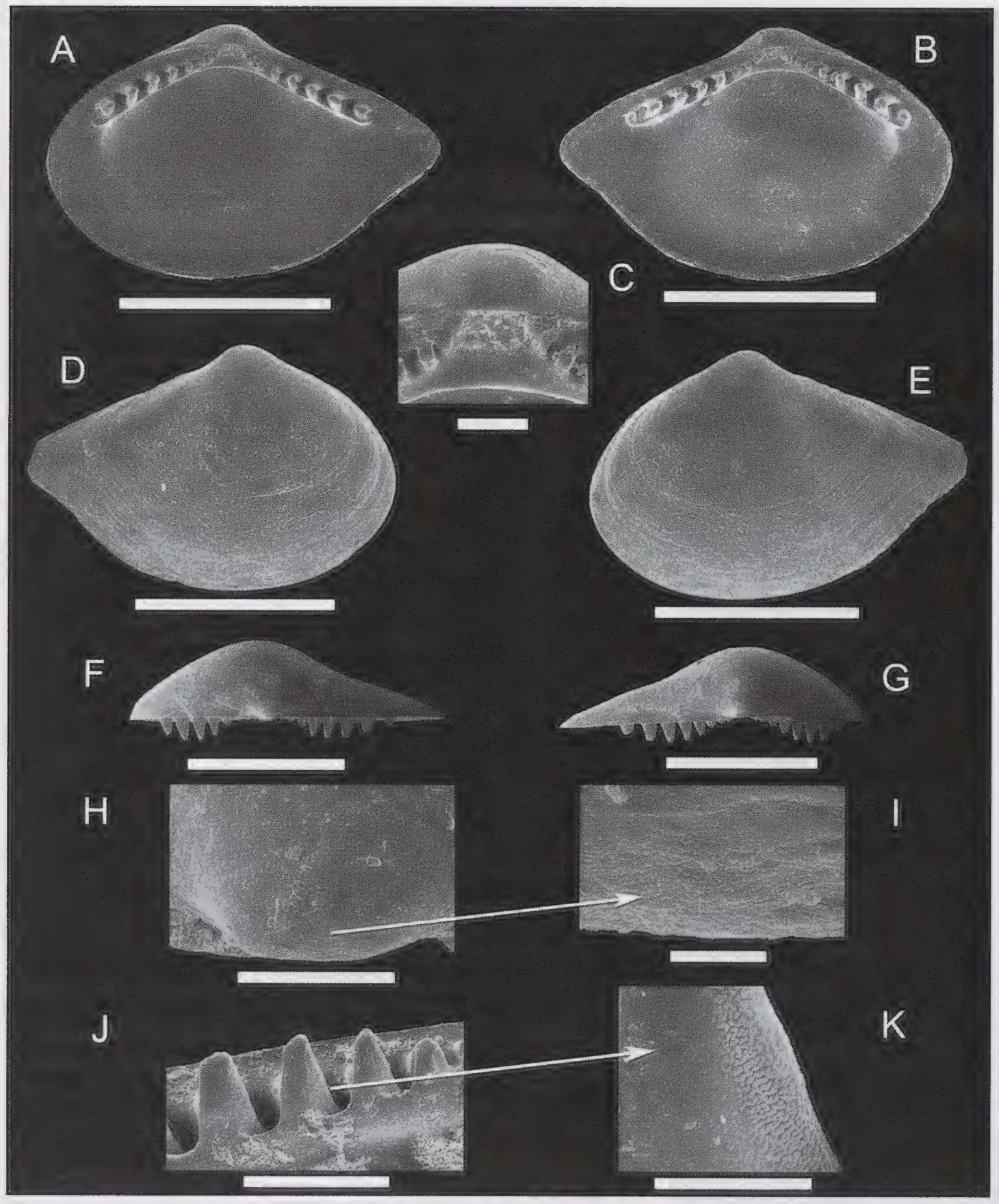


**Figure 8.** *Ledella elfica* sp. nov. Internal view (Holotype MNRJ 30482): **A,** right valve; **B,** left valve. External view (IBUFRJ 19364): **D,** right valve; **E,** left valve. Dorsal view (IBUFRJ 19363): **F,** right valve; **G,** left valve. Details: **C,** resilifer of the right valve. Prodissoconch (IBUFRJ 19324): **H,** overview; **I,** detail of the tip of the prodissoconch showing some granulation. Hinge teeth (IBUFRJ 19385): **J,** overview; **K,** detail of the tooth showing the tooth pustules. Scales A, B, D–G: 1 mm. C, H: 0.1 mm. I: 0.01 mm. J: 0.2 mm. K: 0.05 mm.

**Material examined** (See supplemental document at: http://www.bioone.org/doi/suppl/10.4003/006.032.0201/suppl_file/Viegas_2014_Suppl_docs.pdf)

**Etymology**

Manati is a Caribbean word for the sea cow. Because sea cows are large, but possess a smooth contour that is similar to the shells of this species, we decided to name it *Ledella manati* sp. nov.

**Distribution**

Known from the Campos Basin, Rio de Janeiro, Brazil and for Trindade Island, Espírito Santo, Brazil.

**Diagnosis**

Thick shell usually without anterior and rostral shoulders, but, when present, not prominent. Rostrum acutely rounded. Shallow rostral sinuosity.

**Description**

Shell oblong–elliptical, inflated, thick, inequivalve, inequilateral, H/L about 0.72; umbones prominent, opisthogyrous and inwardly directed. Antero-dorsal margin convex; anterior margin with a shoulder, rounded ventral margin. Ventral margin forming a shallow sinuosity leading to a rostrate posterior end; postero-dorsal margins lightly convex, sometimes with a weak shoulder near the end of the hinge plate. Smooth surface. Hinge plate interrupted by a deep, rounded resilifer. Posterior hinge plate longer and thinner than anterior one in adult specimens, and almost equal in juveniles. Width of the anterior and posterior rows of teeth occupying about 59% and 58%, respectively, of the total width of the hinge plate of the right valves and 61% and 57% to the anterior and posterior hinge plates, respectively, of the left valve. Shell microsculpture: the prodissoconch presents a weak granulation and the hinge teeth present pustules on the side that faces the umbones. Maximum shell length 2.02 mm. Prodissoconch height: 90 μm. Prodissoconch length: 118 μm. (Table 4)

**Remarks**

*Ledella manati* sp. nov. differs from *L. semen* in having less opisthogyrous umbones and a less acute rostrum than *L. semen.*

*Ledella manati* sp. nov. differs from *L. solidula* in having no concentric lines and a rostrum that is shorter and less acute than that of *L. solidula.*

*Ledella manati* sp. nov. differs from *L. ultima* in having no concentric lines and in presenting thinner teeth on the hinge plate and a more acute rostrum than *L. ultima.*

*Ledella manati* sp. nov. differs from *L. acinula* in having no concentric lines and in presenting a more acute rostrum and a less inflated posterior region of the shell than *L. acinula.*

*Ledella manati* sp. nov. differs from *L. orixa* in presenting less opisthogyrous umbones, a larger posterior region than the anterior region and a smaller anterior part of the hinge plate when compared to the posterior part.

*Ledella manati* sp. nov. is similar to *L. sublevis* in having a shallow rostral sinuosity, a smooth surface and a thick shell, but *L. manati* sp. nov. can be distinguished by its less acute rostrum and thinner hinge teeth.

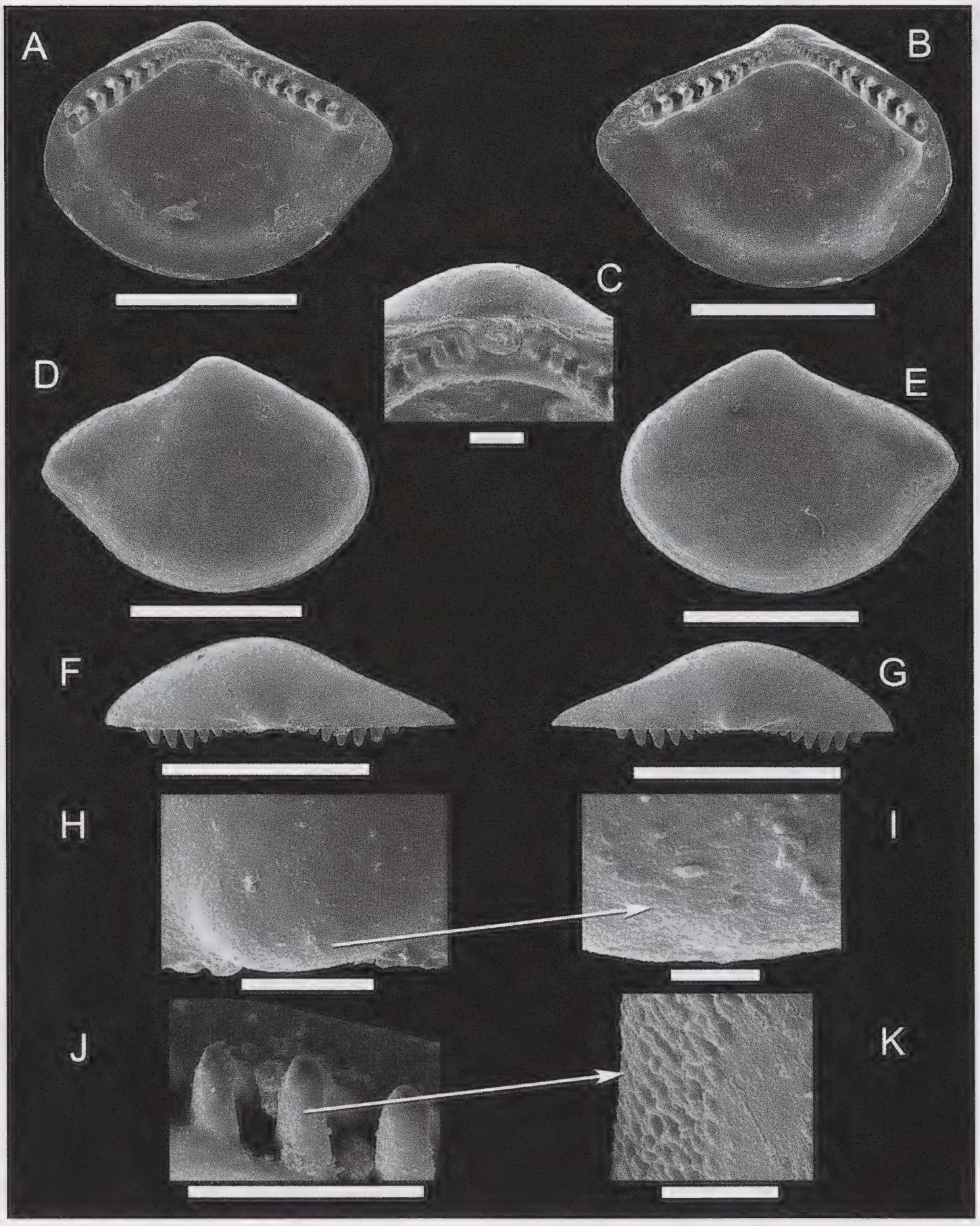


**Figure 9.** *Ledella manati* sp. nov. Internal view (Holotype MNRJ 30483): **A,** right valve; **B,** left valve. External view (IBUFRJ 19435): **D,** right valve; **E,** left valve. Dorsal view (IBUFRJ 14673): **F,** right valve; **G,** left valve. Details: **C,** resilifer of the right valve. Prodissoconch (IBUFRJ 14637): **H,** overview; **I,** detail of the tip of the prodissoconch showing some granulation. Hinge teeth: **J,** overview; **K,** detail of the tooth showing the tooth pustules. Scales A, B, D–G: 1 mm. C, H: 0.1 mm. I: 0.02 mm. J: 0.2 mm. K: 0.01 mm.

*Ledella manati* sp. nov. is similar to *Ledella verdiensis* Allen and Hanna, 1989 in having a similar shell shape with a shallow rostral sinuosity, but it can be distinguished on the basis of having no strong concentric lines, a less high shell, a thicker hinge plate and a smoother postero-dorsal margin than *L. verdiensis*.

*Ledella manati* sp. nov. differs from *L. spocki* sp. nov. in having a shorter and less acute rostrum, with a rostral sinuosity that is about half the profundity as that of *L. spocki* sp. nov., and a longer and thinner anterior part of the hinge plate in relation to the shell size, but a shorter posterior part of the hinge plate with no thickness difference to that of *L. spocki* sp. nov. The prodissoconch of *L. manati* sp. nov. is larger than that of *L. spocki* sp. nov. in both height and length, but there is no difference regarding its microsculpture.

*Ledella manati* sp. nov. differs from *L. legionaria* sp. nov. in having a longer and higher rostrum, with a rostral sinuosity that is about half the profundity as that of *L. legionaria* sp. nov. on the left valve, but about 66% less profound on the right valve. *Ledella manati* sp. nov. also has a longer and thinner anterior part of the hinge plate, but a shorter and thicker posterior part when compared to *L. legionaria* sp. nov. The hinge teeth occupy almost the same proportion of the hinge plate thickness in both species. Regarding the prodissoconch, they do not differ much in height and microsculpture, but the prodissoconch of *L. manati* sp. nov. is larger in length than the prodissoconch of *L. legionaria* sp. nov.

*Ledella manati* sp. nov. differs from *L. elfica* sp. nov. inhaving a shorter and less acute rostrum, with a rostrum sinuosity with about half the profundity as that of *L. elfica* sp. nov. Additionally, *L. manati* sp. nov. has a shorter and thicker posterior part of the hinge plate, but an anterior part with no difference in length or thickness compared to *L. elfica* sp. nov. Regarding the prodissoconch, they do not differ much in height and microsculpture, but the prodissoconch of *L. manati* sp. nov. is larger in length than the prodissoconch of *L. elfica* sp. nov.

## DISCUSSION

One of the major problems associated with the traditional taxonomical approach is its subjectivity, which generates a relationship of dependency between the expertise of the taxonomist and the reliability of the taxonomical decisions. In general, the taxonomist notes, somewhat intuitively, many differences between the taxa he is working on. The main difficulty lies in making these differences clear to the readers. The morphometric approach itself does not solve this problem, because the taxonomist cannot handle the distinct measurements taken from all over the shell to determine which ones are relevant for discriminating among the taxa. A technique to reduce this myriad of potentially important variables to a manageable number of morphologically understandable factors is fundamental for obtaining objectivity in taxonomic

**Table 4.** Average values of the larval shell measurements and length of the adult shell. H(p) – Height of the prodissoconch I; *SD*, standard deviation; L(p), Length of the prodissoconch I; *n*, number of measured valves; L (s), Length of the adult shell; Min, Minimum value; Max, Maximum value.

| | H(p) | *SD* | L(p) | *SD* | *n* | L (s) | Min | Max | *n* |
|---|---|---|---|---|---|---|---|---|---|
| *Ledella spocki* sp. nov. | 0,071 | 0,005 | 0,073 | 0,004 | 20 | 1,674 | 1,336 | 1,937 | 60 |
| *Ledella legionaria* sp. nov. | 0,078 | 0,006 | 0,086 | 0,004 | 20 | 1,891 | 1,367 | 2,318 | 60 |
| *Ledella elfica* sp. nov. | 0,083 | 0,006 | 0,104 | 0,004 | 20 | 1,632 | 1,291 | 1,869 | 60 |
| *Ledella manati* sp. nov. | 0,091 | 0,004 | 0,118 | 0,003 | 20 | 1,708 | 1,401 | 2,027 | 60 |

work. The discriminant analysis is not the only statistical technique that is able to do this, but the method has a clear and simple mathematical basis (Klecka 1982). In our case, it reduced the original 44 variables to a few comprehensible factors.

Considering the right valves, the variables Prs, Lr and Hrd/Hrv, which are all related to the rostrum, were found to be critical characters in discriminating among these species. Moreover, a complementary set of variables (wap, wap/ahp, wpp, hpt, and hpt/W), which are all related to the hinge plate, was shown to be critical for discrimination. An additional set of morphological variables providing minor contributions completed the analysis. The rate of agreement between traditional taxonomy and this morphometric-based approach was 95%.

Analysis of the left valves produced similar results. Due to differences between right and left valves within the same specimen (inequivalve condition), a somewhat different set of variables was selected to maximize the distinction among the four taxa. The most relevant variables were: W, lhp/L, W/L, alm and R2. This set of variables carries information about the general shape of the valve, in contrast to the right valves analysis, which indicated different characters as being important. In the left valves analysis, the rate of agreement between traditional taxonomy and this morphometric-based approach was 88.33%.

The second set of analyses, which was based on hinge plate characters alone, revealed the importance of these features for distinguishing the four species: the rates of agreement between traditional taxonomy and this morphometric-based approach were 66.66% for the right valves and 64.16% for the left valves. This finding corroborates the importance of including the hinge plate structure in morphometric analysis, as stated by Benaim *et al.* (2011) in their study of *Yoldiella* species. This outcome is not surprising because hinge characters were important in the complete morphometric analyses performed earlier in this study. However, despite being highly important, the hinge plate characters alone have a lower rate of agreement between the traditional taxonomical approach and the morphometric approach than the analyses using the full set of morphometric variables. In other words, the variables that are associated with the shell (valve) shape are essential for producing a satisfactorily high rate of agreement between traditional taxonomy and this morphometric-based approach.

The larval shell of these species present some microsculpture. The prodissoconch I presents a weak granulation (Figs. 6H, 6I, 7H, 7I, 8H, 8I,9H and 9I) that cannot be perceived without the use of an electron microscope. The nepioconch cannot be clearly defined for these species, because either it is undifferentiated from the adult shell or it does not present a clear boundary with it.

Regarding the prodissoconch, it is also important to notice that the prodissoconch I of these species are smaller than expected for protobranchs (Gustafson and Reid 1986) and, since the prodissoconch II is not visible, it probably means that the eggs are brooded or lecithotrophic (Zardus and Martel 2002). Since no brooding was observed in the samples here analyzed, this suggests these species simply have rather small eggs.

The SEM images also revealed the presence of microsculpture on the hinge teeth of all four species described herein (Figs.6J, 6K, 7J, 7K, 8J, 8K, 9J and 9K). Malchus and Sartori (2012) describe similar teeth pustules in Nuculanidae, but the origin and function of these pustules are unknown (Malchus, pers. comm.). They may generate more attrition between the teeth, so that they are harder to slide, turning the shell harder to open by predators, but a study about its function must be done prior to defining its actual function. This information is not mentioned for the other *Ledella* species to which we compare our species, but we do not know if it is present or not, since the detection of this character is very specific and was not done for the other species yet.

## CONCLUSIONS

The description of these four species improves the understanding of the biodiversity of protobranchs of the Campos Basis, contributes with some morphological aspects of *Ledella* species and corroborates the importance of including specific hinge plate details in the characterization of protobranch species.

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